VARIATION IN THE HORIZONTAL DISTRIBUTION OF PLANKTON IN DEVILS LAKE, NORTH DAKOTA

ERIK G. MOBERG[1]

The horizontal distribution of plankton has been studied by several investigators and varied results have been obtained. It is usually held, however, that under uniform physical conditions the distribution of the plankton is uniform. The question is of great importance since in quantitative plankton investigations the amount of plankton found at a certain station is usually taken as representative of a large area.

For several years plankton studies have been carried on at the Biological Station at Devils Lake, North Dakota, under the direction of Dr. R. T. Young, and in connection with these studies collections were made during the summer of 1914, to determine whether the organisms in Devils Lake showed any diurnal movements. For this purpose collections were made shortly after noon, just after sunset, and shortly before sunrise from the surface, the 0.6 m., the 2.1 m., and the 3.6 m. levels, the depth of the lake at that place being about 4 m. All the samples were taken in identically the same place and on all occasions the velocity of the wind and the condition of the sky were similar. The samples, each of 500 cc., were concentrated to 10 cc., and counted according to the Sedgwick-Rafter[2] method. In each case the total number of individuals in two or three cells, and therefore in 100 cc. or 150 cc. of the original sample, were counted. The results obtained are shown in Table I.

TABLE I

SHOWING THE NUMBER OF INDIVIDUALS PER LITER OF WATER

	1:00–2:30 P.M.		8:30–9:30 P.M.		3:00–4:00 A.M.	
Depth	Crustacea	Rotifera	Crustacea	Rotifera	Crustacea	Rotifera
Surface	40	310	110	770	160	480
0.6 m	20	440	90	920	240	560
2.1 m	25	380	95	680	280	360
3.6 m	125	330	270	940	260	580
Total all levels	210	1460	565	3310	940	1980

[1] Numerals refer to notes beginning on p. 265.

Even if there had been a vertical movement of the organisms the total number of individuals of one series should be approximately equal to that of another series. Instead we find that the evening series contains more than twice as many crustaceans as the noon series, and that collected in the morning more than four times as many. In the case of the rotifers the variations are not quite as large. These results seem to show that there had been horizontal movements of the plankton animals during the intervals between the periods of collecting.

To test the horizontal distribution further and more directly several series of collections were made during the summers of 1914, 1915 and 1916. In some cases the samples were taken from a number of nearby points in a part of the lake where the physical conditions do not vary appreciably, while in others the entire series was collected from a fixed point at short intervals of time. The accompanying maps show the main part of the lake and the approximate locations of the stations at which the samples were obtained.

In connection with some of the 1915 series the amount of phytoplankton and of dissolved chemicals (oxygen, free and albuminoid ammonias, and CO^3 and HCO^3 ions) were determined[3] in order to show the relation between the zooplankton and the food and chemical constituents in the water.

During 1914 and 1915 the Sedgwick–Rafter method of concentrating and counting was used in the plankton work, ten squares being counted in the case of the plants, but in the case of the animals the entire number of individuals in five cells (one-half of the collection) was counted. Except where specified the volume of each sample was 500 cc. and in all cases it was concentrated to 10 cc. During 1916 the collections were made by means of a pump and a plankton-net. The water was measured by means of a water meter and pumped thru the net where the organisms were retained. Five gallons (18927 cc.) were collected and concentrated to 18.9 cc., making a ratio of 1000 to 1. In five cells of each sample the entire number of zooplanktonts was counted.

The results of the measurements and of the analyses are expressed as follows: depths in meters; temperatures in degrees Centigrade; oxygen in cubic centimeters per liter; ammonias as parts per million of nitrogen; carbonates as parts per million of CO^3 or HCO^3 ions; Nodularia (the only filamentous alga) in number of millimeters per liter; other algae (including Coelospherium, Gomphospheria, Dictyospherium, Chroococcus,

Merismopedia, and a number of others, less common), in standard units[4] per liter; diatoms, rotifers, and crustaceans in number of individuals per liter.

The variation in the horizontal distribution of the plankton may be studied from three different points of view; namely: (1) the variation of the total amount of plankton, (2) the variation of each species, and (3) the correlation between the zooplanktonts, the phytoplanktonts, and the physical and chemical conditions of the environment.

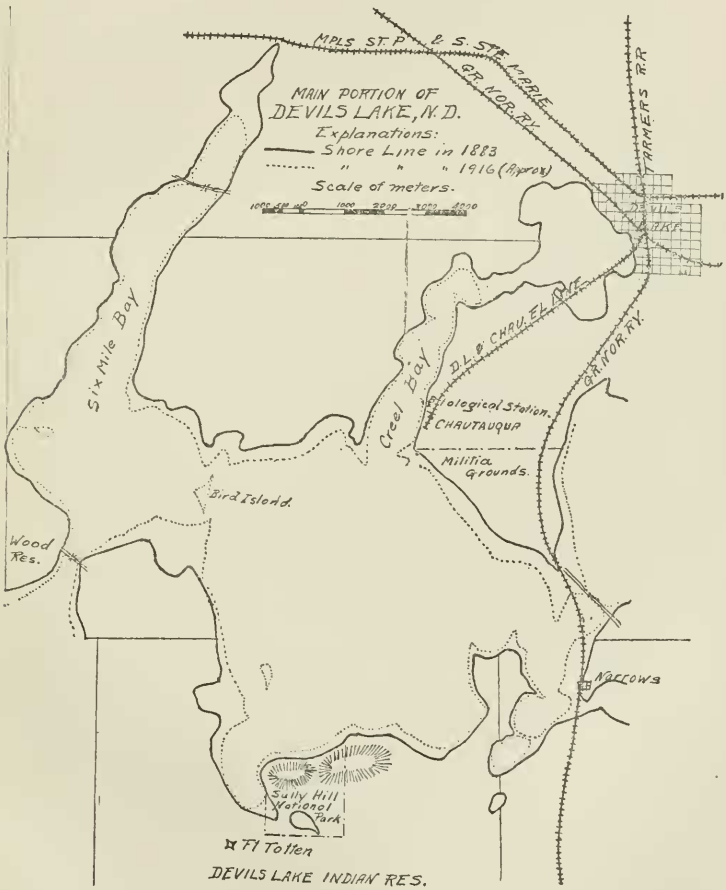

FIGURE 1

The Sedgwick–Rafter method hardly lends itself to the study of the total amount of plankton but it may be roughly estimated by considering the occurrence of the more important species. The number of individuals of the different species, however, may be determined quite closely.

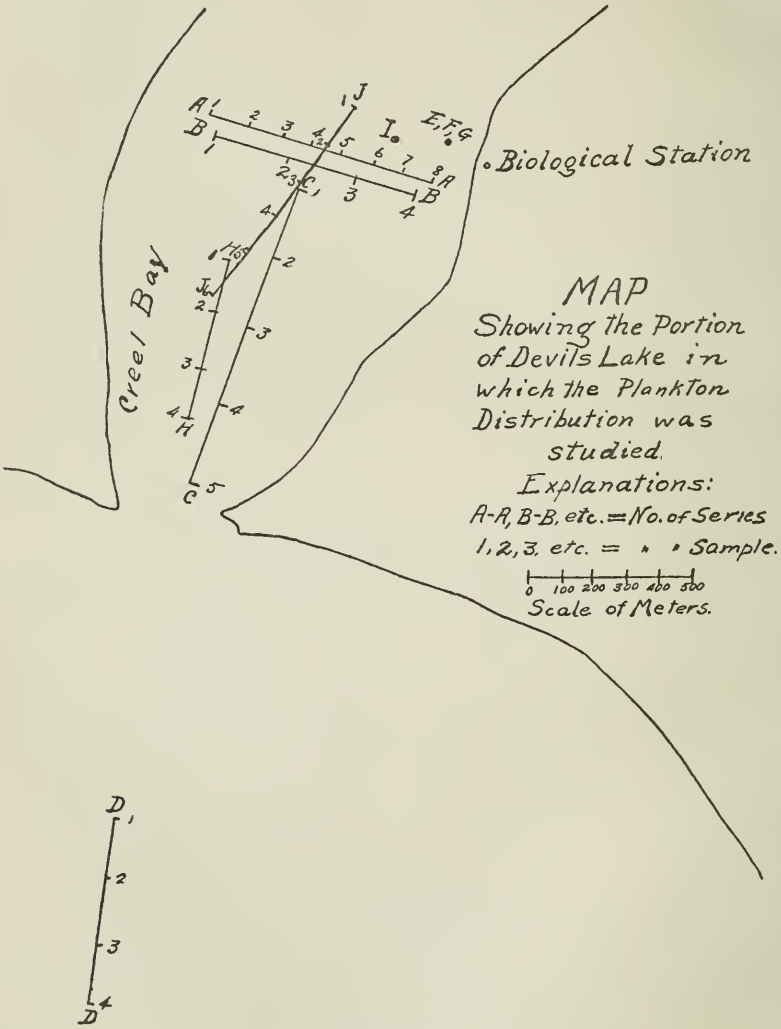

FIGURE 2

Whipple[5] states that the experimental error is not more than about ten per cent. In the case of some of the algae, the error is probably larger, especially since only ten squares were counted, and in considering the results this should be remembered; but for the animals it is probably less since a large portion of the sample was examined. Since in most cases the depth and the temperature were measured and the amount of chemicals determined, the results give some conception of the relation between the plankton and the environment. It must be remembered, however, that some of the variation in the chemicals is due to experimental error.

Notes on the Different Collections and Tabulation of Results

Series A. A set of eight samples was collected on August 19, 1914 from points lying in a straight line between the two shores of Creel Bay The distance between each two points was about 100 meters and the time required for the whole series was about a half hour. The greatest depth between the two shores was 4.5 meters at points 5 and 6. At no point does the depth vary more than one meter and the character of the bottom is uniform, the points 1 and 8 being outside the littoral zone. At the time of collecting the sky was clear and there was almost no wind. Only the animals were counted and the results are shown in Table II.

TABLE II

Showing Data for Series A

(Amt. = Amount. % var. = variation from the mean in per cent)

	Sample 1		Sample 2		Sample 3		Sample 4	
	Amt.	% var.	Amt.	% var.	Amt.	% var.	Amt.	% var.
Temperature	21.8	+3.3	21.5	+1.9	21.0	−0.4	21.0	−0.4
Brachionus satanicus	108	−39.7	48	−73.2	128	−28.4	140	−21.8
Brachionus mülleri	44	+62.9	40	+48.1	36	+33.3	24	−11.1
Pedalion	248	−32.6	540	+46.7	300	−18.5	324	−11.9
Moina	104	−13.3	40	−66.6	16	−86.6	92	−23.3
Cyclops	16	+10.3	4	−69.2	4	−69.2	24	+84.6
Diaptomus	0	−100.0	4	+100.0	8	+300.0	0	−100.0
Nauplii	80	+66.6	36	−25.0	28	−41.7	48	0.0

TABLE II (*Continued*)

	Sample 5		Sample 6		Sample 7		Sample 8		
	Amt.	% var.	Amt.	% var.	Amt.	% var.	Amt.	% var.	Mean
Temperature	20.8	−1.4	20.8	−1.4	21.0	−0.4	21.8	+3.3	21.1
Brachionus satanicus	356	+98.9	292	+63.1	200	+11.7	160	−10.5	179.0
Brachionus mülleri	16	−40.7	36	+33.3	4	−85.1	16	−40.7	27.0
Pedalion	564	+53.2	372	+1.1	372	+1.1	224	−39.1	368.0
Moina	44	−63.3	148	+23.3	144	+20.0	372	+210.0	120.0
Cyclops	24	+84.6	28	+93.1	4	−69.2	12	−7.6	14.5
Diaptomus	4	+100.0	0	−100.0	0	−100.0	0	−100.0	2.0
Nauplii	84	+75.0	48	0.0	16	−66.6	44	−8.3	48.0

These analyses show a large variation of all the species and especially of the Crustacea. The total number of animals is almost constant, however, since one form is numerous where another is scarce. The temperature varies one degree but does not seem to have any effect on the number of animals. The variations shown by the different species are summarized in Table III.

TABLE III

PERCENT OF VARIATION FROM MEAN OF SERIES A

	Mean	Maximum	Minimum	Range
Brachionus satanicus	±43.4	+98.9	−73.2	172.1
Brachionus mülleri	±44.4	+62.9	−85.1	148.0
Pedalion	±25.5	+53.2	−39.1	92.3
Moina	±63.3	+210.0	−86.6	296.6
Cyclops	±61.0	+93.1	−69.2	162.3
Nauplii	±35.4	+75.0	−66.6	141.6

Series B. These samples were collected on August 25, 1914, in the same locality and under the same weather conditions as those of series A, but the distances between the different points of series B were about twice as large, and 1000 cc., instead of 500 cc., were concentrated. No separate counts were made of the different species but the animals are grouped under Crustacea and Rotifera. The Crustacea include: Moina,

Diaptomus, Cyclops, and Copepod Nauplii. The Rotifera include: *Brachionus satanicus, B. mülleri,*[6] Pedalion, and a few Asplanchna. The results are shown in Table IV.

TABLE IV

SHOWING DATA FOR SERIES B

(Amt.=amount. % var.=variation from mean in per cent)

	Sample 1		Sample 2		Sample 3		Sample 4		
	Amt.	% var	Amt.	% var.	Amt.	% var.	Amt.	% var.	Mean
Temperature	15.8		15.8		15.8		15.2		
Crustacea	198	−44.7	355	−0.8	552	+54.2	326	−8.9	358
Rotifera	162	−46.2	427	+41.8	316	+4.9	298	−1.0	301

For the Rotifera the mean variation from the average is ±23.4% the maximum variation +42%, and the minimum variation −45.7%, making a range of 87.7%. For the Crustacea the figures are: mean ±27.1%, maximum +54.3%, minimum −44.6%, range 98.9%. Here again the crustaceans show a larger variation than the rotifers, altho the former are more numerous.

Series C. This series was collected on June 6, 1915, from points lying in a straight line parallel to the shores of Creel Bay, point 1 lying just south of where the collections of series A and B were made, and point 5 a short distance inside the mouth of the bay. The sky was clear, the time required about one hour, and the distance between each two points about 250 meters. The results are shown in Table V.

The very slight variation in depth shows no effect upon the organisms. The chemicals, excepting the ammonias, show a uniform distribution, the variations not being greater than the errors of sampling and analysing. None of the plankton forms, nor the plankton as a whole, show any relation to the amount of ammonias. It may be noted that most of the forms were scarce at point 1, and abundant at point 5, but at the intervening points the total amount of plankton appears quite constant. Table VI summarizes the variation of the different plankton forms.

TABLE V

DATA FOR SERIES C

(Abbreviations as in previous tables)

	Sample 1		Sample 2		Sample 3		Sample 4		Sample 5		
	Amt.	% var.	Amt.	% var.	Amt.	% var.	Amt.	% var.	Amt.	% var.	Mean
Depth	4.6	−9.8	4.6	−9.8	5.2	+1.9	5.5	+7.8	5.5	+7.8	5.1
Free Ammonia	0.135	+3.0	0.126	−3.8	0.076	−42.0	0.190	+45.0	0.130	−0.8	0.131
Albuminoid Ammonia	0.96	−15.0	1.76	+55.8	0.81	−28.3	1.13	0.0	1.00	−11.5	1.13
Oxygen	6.2	.....	6.2	.....	6.3	.....	.....	.....	6.2	.....	.....
CO_3ion	266	+9.7	272	+12.2	213	−12.2	213	−12.2	248	+2.3	242.4
HCO_3ion	601	−2.4	590	−4.2	642	+4.2	642	+4.2	604	−1.9	616
Nodularia spumigena	86,000	+1.4	164,000	+93.4	46,000	−45.7	70,000	−17.5	58,000	−31.6	84,800
Other Algae	182,000	−49.2	456,000	+27.3	218,000	−39.1	374,000	+4.5	558,000	+55.9	358,000
Brachionus satanicus	12	−53.1	20	−21.9	24	−6.3	32	+25.0	40	+56.2	25.9
Brachionus mülleri	20	+66.6	8	−33.3	12	0.0	16	+33.3	4	−66.6	12
Pedalion fennicum	128	−41.3	168	−22.9	328	+50.5	196	−10.1	272	+24.8	218
Asplanchna sylvestri	0	−100.0	12	−6.2	16	+25.0	8	−37.5	28	+118.7	12.8
Cyclops viridis	12	−40.0	16	−20.0	28	+40.0	8	−60.0	36	+80.0	20
Diaptomus sicilis	96	−11.1	180	+66.6	88	−18.5	72	−33.3	104	−3.7	108
Nauplii	60	−45.6	160	+44.9	152	+37.7	108	−2.1	72	−34.7	110.4

TABLE VI

PRECENT OF VARIATION FROM MEAN OF SERIES C

	Mean	Maximum	Minimum	Range
Nodularia	±37.9	+93.4	−45.7	139.1
Other Algae	±35.2	+55.9	−49.2	105.1
Brachionus satanicus	±32.5	+56.2	−53.1	109.3
Brachionus mülleri	±40.0	+66.6	−66.6	133.2
Pedalion	±29.9	+50.5	−41.1	91.8
Asplanchna	±57.5	+118.7	−100.0	218.7
Cyclops	±48.0	+80.0	−60.0	140.0
Diaptomus	±26.6	+66.6	−33.3	99.9
Nauplii	±33.0	+44.9	−45.6	90.5

Series D. This series was collected on June 21, 1915, well out in the main part of the lake as shown on the map. A very slight south-west wind was blowing and the sky was clear. The time required was about one hour and the distance between two points about 200 meters. Table VII shows the results.

These analyses show a uniformity of physical and chemical conditions, except in the case of the free ammonia which varies to an unusual extent. Since it is present in small amounts it is probable that the greater part of its variation is due to experimental error. No relation is shown between the amount of ammonia and the amount of plankton. All the animals, and especially the adult crustaceans, occur in small numbers, so that some of them will be excluded in tabulating the variation percentages. It is important to note that at point 3 all animals, except Cyclops and the nauplii, are absent, while at point 4 most of them are quite numerous. The summary of the variations is shown in Table VIII.

TABLE VIII

PERCENT OF VARIATION FROM THE MEAN OF SERIES D

	Mean	Maximum	Minimum	Range
Nodularia	±51.9	+61.2	−72.1	133.3
Other Algae	±11.1	+22.3	−14.6	36.9
Brachionus satanicus	±138.1	+276.2	−100.0	376.2
Brachionus mülleri	±81.8	+118.2	−100.0	218.2
Pedalion	±57.1	+77.1	−100.0	177.1
Nauplii	±50.0	+100.0	−80.0	180.0

TABLE VII

DATA FOR SERIES D

(Abbreviations as in previous tables)

	Sample 1		Sample 2		Sample 3		Sample 4		
	Amt.	% var.	Amt.	% var.	Amt.	% var.	Amt.	% var.	Mean
Depth	5.8	+1.8	5.8	+1.8	5.6	−1.8	5.5	−3.5	5.7
Temperature	20.0		20.0		20.3		20.3		
Oxygen	6.46	−0.9	6.55	+0.5	6.55	+0.5			6.52
Free Ammonia	0.20	+100.0	0.10	0.0	0.06	−40.0	0.06	−40.0	0.10
Albuminoid Ammonia	0.94	+8.0	0.91	+4.6	0.80	−8.0	0.84	−3.4	0.87
CO_3ion	226	−4.2	236	0.0	243	+3.0	239	+1.3	236
HCO_3ion	608	−0.5	585	−4.3	581	−4.9	670	+9.6	611
Nodularia spumigena	44,000	−31.8	104,000	+61.2	92,000	+42.6	18,000	−72.1	64,500
Other Algae	152,000	−3.2	192,000	+22.3	150,000	−4.5	134,000	−14.6	157,000
Brachionus satanicus	16	−84.2	8	−92.1	0	−100.0	380	+276.2	101
Brachionus mülleri	24	+118.2	4	−63.6	0	−100.0	16	+45.4	11
Pedalion fennicum	60	−14.3	96	+37.1	0	−100.0	124	+77.1	70
Asplanchna sylvestri	0	+100.0	0	−100.0	0	−100.0	4	+300.0	1
Cyclops viridis	0	−100.0	0	−100.0	12	+200.0	4	0.0	4
Diaptomus sicilis	16	+300.0	0	−100.0	0	−100.0	0	−100.0	4
Nauplii	20	0.0	40	+100.0	4	−80.0	16	−20.0	20

Series E. This series was collected on July 27, 1915, from an anchored raft some distance from the shore, where the depth was about four meters. The four samples were taken at fifteen minute intervals beginning at 11:30 A.M. and continuing until 12:15 P.M. The wind was blowing from the south causing small waves, which increased in size toward the end of the series. Cloudiness and sunshine alternated at short intervals thruout the period. The results of the analyses are shown in Table IX.

The temperature and the chemicals are almost constant. The first sample shows a small amount of both plants and animals while in sample 4 the zooplanktonts are abundant. Table X summarizes the percentages.

TABLE X

PERCENT OF VARIATION FROM MEAN OF SERIES E

	Mean	Maximum	Minimum	Range
Nodularia	±10.8	+10.5	−21.5	32.0
Other Algae	±7.0	+14.0	−9.0	23.0
Chaetoceros	±34.7	+36.1	−42.9	79.0
Other diatoms	±69.5	+139.0	−65.9	204.9
Brachionus satanicus	±39.3	+78.6	−41.2	119.8
Brachionus mülleri	±28.2	+54.3	−54.3	108.6
Pedalion	±17.8	+35.6	−16.3	51.9
Cyclops	±25.0	+50.0	−50.0	100.0
Diaptomus	±50.0	+75.0	−100.0	175.0
Nauplii	±55.2	+73.1	−70.1	143.2

Series F and G. These two series were collected on August 3, 1915, at the same point as was series E. Series F represents samples taken from the surface, while the samples of series G were taken from a depth of three meters. The samples of the two series were taken alternately at fifteen minute intervals, the period between the collecting of two samples of the same series therefore being a half hour. The first collection was made at 2:00 P.M. The sky was clear and there was almost no wind. The results of the analyses of series F are shown in Table XI.

These analyses show the physical and chemical factors to be quite constant, and the total amount of plankton seems fairly evenly distributed, except in 1 where all the animals and most of the plants are absent or few in number. The results are summarized in Table XII.

TABLE IX

DATA FOR SERIES E

(Abbreviations as in previous tables)

	Sample 1		Sample 2		Sample 3		Sample 4		
	Amt.	% var.	Amt.	% var.	Amt.	% var.	Amt.	% var.	Mean
Oxygen	.....	.....	.....6.36	+1.1	6.16	−2.1	6.37	+1.1	6.29
Free Ammonia	0.04	0.0	0.04	0.0	0.04	0.0	0.04	0.0	0.04
Albuminoid Ammonia	1.00	+5.2	0.90	−5.2	0.90	−5.2	1.00	+5.2	0.95
CO_3 ion	258	+4.9	233	−5.3	251	−2.0	243	−1.2	246
HCO_3 ion	590	+0.9	598	+2.2	576	−1.5	574	−1.9	585
Nodularia spumigena	112,000	−21.5	152,000	+6.2	150,000	+4.9	158,000	+10.5	143,000
Other Algae	174,000	−4.7	182,000	−0.3	208,000	+14.0	166,000	−9.0	182,500
Chaetoceros elmorei	100,000	+36.1	54,000	−26.5	98,000	+33.3	42,000	−42.9	73,500
Other Diatoms	98,000	+139.0	20,000	−51.2	32,000	−21.9	14,000	−65.9	41,000
Brachionus satanicus	332	−11.2	276	−26.2	668	+78.6	220	−41.2	374
Brachionus mülleri	84	−54.3	180	−2.2	188	+2.2	284	+54.3	184
Pedalion fennicum	200	−16.3	224	−6.3	208	−13.0	324	+35.6	239
Cyclops viridis	12	−50.0	36	+50.0	24	0.0	24	0.0	24
Diaptomus sicilis	0	−100.0	16	0.0	28	+75.0	20	+25.0	16
Nauplii	92	+37.3	40	−40.3	20	−70.1	116	+73.1	67

TABLE XI

DATA FOR SERIES F

(Abbreviations as in previous tables)

	Sample 1		Sample 3		Sample 5		Sample 7		
	Amt.	% var.	Amt.	% var.	Amt.	% var.	Amt.	% var.	Mean
Temperature	20.5	−1.9	20.5	−1.9	21.3	+1.9	21.3	+1.9	20.9
Oxygen	6.3	0.0	6.2	−1.6	6.3	0.0	6.4	+1.6	6.3
Free Ammonia	0.02	0.0	0.02	0.0	0.02	0.0	0.02	0.0	0.02
Albuminoid ammonia	0.40	−20.0	0.40	−20.0	0.60	+20.0	0.60	+20.0	0.50
CO_3 ion	179	−12.3	195	−4.4	214	+4.9	228	+11.8	204
HCO_3 ion	674	+4.7	665	+3.3	631	−2.0	608	−5.6	644
Nodularia spumigena	296,000	+44.4	190,000	−7.3	160,000	−21.9	174,000	−15.1	205,000
Other Algae	90,000	−37.1	182,000	+27.2	162,000	+13.3	138,000	−3.5	143,000
Chaetoceros elmorei	30,000	−78.3	130,000	−5.8	252,000	+82.6	140,000	−1.4	138,000
Other diatoms	14,000	+27.3	14,000	+27.3	14,000	+27.3	2,000	−81.8	11,000
Brachionus satanicus	80	−23.8	128	+21.9	110	+4.8	104	−0.9	105
Pedalion fennicum	36	−80.7	76	−59.4	340	+81.8	296	+58.3	187
Cyclops viridis	0	−100.0	16	+60.0	16	+60.0	8	−20.0	10
Diaptomus sicilis	0	−100.0	0	−100.0	0	−100.0	8	+300.0	2
Nauplii	8	−55.5	20	+11.1	40	+122.2	4	−77.7	18

TABLE XII

PERCENT OF VARIATION FROM MEAN OF SERIES F

	Mean	Maximum	Minimum	Range
Nodularia	±22.2	+44.4	−21.9	66.3
Other Algae	±20.3	+27.2	−37.1	64.3
Chaetoceros	±42.0	+82.6	−78.3	160.9
Other Diatoms	±40.9	+27.3	−81.8	109.1
Brachionus satanicus	±12.8	+21.9	−23.8	45.7
Pedalion	±70.0	+81.8	−80.7	162.5
Cyclops	±60.0	+60.0	−100.0	160.0
Nauplii	±66.6	+122.2	−77.7	199.9

Table XIII shows the results of the analyses of series G. Here the total amount of plankton varies considerably since the variation of the different species is more or less parallel. The chemicals are quite constant. A summary of the variation of the different plankton forms is shown in Table XIV.

Series H. Since in the previous collections comparatively few crustaceans had been obtained, it was decided to collect larger samples. On October 15, 1915, four samples were therefore collected from approximately the same points as those of series C during clear and almost perfectly calm weather. Two liters of each sample were filtered thru fine bolting cloth. This allowed the diatoms and some of the algae to pass thru but retained all the crustaceans and rotifers. This was determined

TABLE XIV

PERCENT OF VARIATION FROM MEAN OF SERIES G

	Mean	Maximum	Minimum	Range
Nodularia	±26.4	+50.0	−47.4	97.4
Other Algae	±37.0	+74.0	−47.1	121.1
Chaetoceros	±50.8	+51.6	−81.3	132.9
Other Diatoms	±36.8	+57.9	−36.8	94.7
Brachionus satanicus	±34.7	+47.8	−62.5	110.3
Pedalion	±78.2	+153.7	−86.0	239.7
Cyclops	±35.1	+65.2	−43.5	108.7
Diaptomus	±50.0	+100.0	−50.0	150.0
Nauplii	±63.6	+78.2	−92.7	170.9

TABLE XIII

DATE FOR SERIES G

(Abbreviations as in previous tables)

	Sample 2		Sample 4		Sample 6		Sample 8		
	Amt.	% var.	Amt.	% var.	Amt.	% var.	Amt.	% var.	Mean
Oxygen	6.0	+1.6	6.2	+1.6	6.2	+1.6	6.1	0.0	6.1
Free Ammonia	0.02	0.0	0.02	0.0	0.02	0.0	0.02	0.0	0.02
Albuminoid Ammonia	0.40	−20.0	0.40	−20.0	0.60	+20.0	0.60	+20.0	0.50
CO_3 ion	219	−3.9	217	−4.8	199	−12.7	277	+21.5	228
HCO_3 ion	618	−0.5	622	−0.2	645	+3.9	601	−3.2	621
Nodularia	78,000	+2.6	114,000	+50.0	40,000	−47.4	72,000	−5.3	76,000
Other Algae	104,000	−47.1	342,000	+74.0	172,000	−12.5	168,000	−14.5	196,500
Chaetoceros	102,000	−20.3	192,000	+50.0	24,000	−81.3	194,000	+51.6	128,000
Other Diatoms	30,000	+57.9	12,000	−36.8	12,000	−36.8	22,000	+15.8	19,000
Brachionus satanicus	1,652	+25.6	1,944	+47.8	493	−62.5	1,172	−10.9	1,315
Pedalion	28	−69.9	236	+153.7	13	−86.0	96	+3.2	93
Cyclops	52	−43.5	96	+4.3	67	−27.2	152	+65.2	92
Diaptomus	32	+100.0	8	−50.0	8	−50.0	16	0.0	16
Nauplii	72	−34.5	164	+49.1	8	−92.7	196	+78.2	110

by an examination of the filtrate. No chemical analysis was made and the plants were not counted. The results are shown in Table XV.

TABLE XV

DATA FOR SERIES H

(Abbreviations as in previous tables)

	Sample 1		Sample 2		Sample 3		Sample 4		
	Amt.	% var.	Amt.	% var.	Amt.	% var.	Amt.	% var.	Mean
Depth	4.6	−10.7	5.2	+1.0	5.3	+2.9	5.5	+6.8	5.15
Temperature	9.5		9.0		9.0		9.0		
Moina	124	+129.6	23	−57.4	47	−13.0	22	−59.3	54
Diaptomus	0	−100.0	4	−48.4	27	+248.4	0	−100.0	7.75
Cyclops	2	−46.7	8	+113.3	3	−20.0	2	−46.7	3.75
Brachionus satanicus	600	+222.6	38	−79.6	64	−65.6	43	−76.9	186.0
Pedalion	8	−38.5	21	+61.5	6	−53.8	16	+23.1	13.0

At point 1 where the depth is the least the temperature is about one-half degree higher than at the other points. At this point, also, Brachionus satanicus and Moina, the most abundant animals, are present in great numbers. Whether this "swarm" was caused by the slight difference in depth and temperature one cannot say, but it is probably only a coincidence, since farther on, where the water was deeper, another swarm of Moina was noticed. The summary is given in Table XVI.

TABLE XVI

PERCENT OF VARIATION FROM MEAN OF SERIES H

	Mean	Maximum	Minimum	Range
Brachionus satanicus	±111.2	+222.6	−79.6	302.2
Pedalion	±44.2	+61.5	−53.8	115.3
Moina	±64.8	+129.6	−59.3	188.9
Cyclops	±56.9	+113.3	−46.7	160.0
Diaptomus	±124.2	+248.4	−100.0	348.4

The distribution of the two sexes of Moina in this series is interesting. On the whole the females are in the majority except at point 2 where the males are about twice as many. At the point immediately preceding,

where a considerable number of Moina is found, the males are totally absent. The following is the detailed distribution:

Point 1	0	males	per	liter	124	females	per	liter.
" 2	15	"	"	"	8	"	"	"
" 3	5	"	"	"	42	"	"	"
" 4	2	"	"	"	20	"	"	"

Series I. In order to obtain still larger volumes of water a series of three samples was collected on August 17, 1916, with the plankton pump at a depth of about two and a half meters from an anchored boat. The weather was calm and when the two last samples were taken the sun went under a thin cloud, which hardly had any effect on the light. Each sample consisted of five gallons (18926 cc.) and was concentrated to 18.9 cc. All the animals in five cubic centimeters of the concentrated sample were counted and the results are shown in table XVII.

TABLE XVII

DATA FOR SERIES I

(Abbreviations as in previous tables

	Sample 1		Sample 2		Sample 3		
	Amt.	% var.	Amt.	% var.	Amt.	% var.	Mean
Asplanchna	3	+30	1	−56.5	3	+30	2.3
Pedalion	73	−12	78	−6	98	+18.1	83.0
Brachionus satanicus	54	+4	54	+4	48	− 8	52.0
Nauplii	55	+10	50	0	45	−10	50.0
Diaptomus	7	+40	3	−40	5	0	5.0
Cyclops	6	+81.8	2	−39.4	2	−39.4	3.3
Moina	0	−100	3	+30	4	+73.9	2.3

In these collections the adult crustaceans are comparatively few, but since a large volume was collected and counted the results may be considered reliable. In the case of the adult crustaceans the variation is large while in the case of the Nauplii and the rotifers it is rather small. The summary of the variation is shown in Table XVIII.

TABLE XVIII

PERCENT OF VARIATION FROM MEAN OF SERIES I

	Mean	Maximum	Minimum	Range
Pedalion	±12	+18.1	−12	30.1
Brachionus satanicus	±5.3	+4	− 8	12.0
Nauplii	±6.7	+10	−10	20.0
Diaptomus	±26.7	+40	−40	80.0
Cyclops	±53.5	+81.8	−39.4	121.2
Moina	±68	+73.9	−100	173.9

Series J. A series of five surface samples were collected on August 27, 1916, from points lying about 100 meters apart in the center of Creel Bay as shown on the map. The lake was perfectly still and had been so for over twelve hours. The volume of each sample and the portions counted were the same as in series I. The results obtained are shown in Table XIX.

These results confirm those already obtained. Diaptomus and Moina are rather numerous, still the variation shown is large. The Nauplii and Rotifera are not as abundant as usual but their distribution is rather uniform. The temperature and the depth are almost constant, and from previous work it may be concluded that the chemicals vary but slightly. Table XX shows the summary of the variation.

TABLE XX

PERCENT OF VARIATION FROM MEAN OF SERIES J

	Mean	Maximum	Minimum	Range
Pedalion	±31.6	+48.4	−45.2	93.6
Brachionus satanicus	±31.1	+55.5	−33.3	88.8
Nauplii	±15.1	+24.5	−35.9	60.4
Diaptomus	±50.2	+112.8	−71.8	184.6
Moina	±25.1	+58.8	−21.6	80.4

TABLE XIX

DATA FOR SERIES J

(Abbreviations as in previous tables)

	Sample 1		Sample 2		Sample 3		Sample 4		Sample 5		
	Amt.	% var.	Amt.	% var.	Amt.	% var.	Amt.	% var.	Amt.	% var.	Mean
Asplanchna	1	.....	0	.....	0	.....	0	.....	0	.....	.....
Pedalion	17	−45.2	41	+32.3	24	−22.6	28	−9.7	46	+48.4	31
Brachionus satanicus	7	−22.2	11	+22.2	6	−33.3	7	−22.2	14	+55.5	9
Nauplii	56	+5.7	66	+24.5	34	−35.9	52	−1.9	57	+7.6	53
Diaptomus	29	−25.6	11	−71.8	43	+10.2	83	+112.8	27	−30.8	39
Cyclops	1	.....	0	.....	1	.....	2	.....	0	.....	.....
Moina	81	+58.8	53	+3.9	40	−21.6	41	−19.6	40	−21.6	51

Discussion of Results

As far as one can tell from the results the total amount of plankton seems to have a quite uniform distribution, except in a few cases where most of the organisms occur in large or small numbers in a certain place or at a certain time. No correlation is shown between the animals and the plant or chemical constituents. Without further investigation it cannot be said, however, that plankton animals are not in any way affected by the amount of phytoplankton or dissolved chemicals. The variation in the latter may be due largely to experimental error. It is probable that if there are variations in their distribution they are small and not likely to cause movements of the plankton animals. The depth and the tmeperature are always nearly constant for the whole series and the small variations that occur do not show any effect on the distribution of the plankton. All of the plankton species show an uneven distribution on all occasions, even when the individuals of a certain species are very numerous. Table XXI gives a summary of the variation of the individual species. The figures are obtained by taking the average of the mean per cent of variation from the mean and of the range of variation of all the series in which the particular species is present in numbers large enough to be considered. The table shows that the crustaceans have the least uniform horizontal distribution, the mean varia-

TABLE XXI

Mean Value and Range of "Percent of Variation from Mean" of All the Series

	No. of series averaged	Mean	Range
Nodularia	5	±29.8	93.6
Other Algae	5	±22.1	70.1
Chaetoceros	3	±42.5	127.0
Other Diatoms	3	±49.1	149.5
Brachionus satanicus	9	±49.8	148.2
Brachionus mülleri	4	±48.6	142.6
Pedalion	9	±40.7	117.1
Asplanchna	1	±57.5	218.7
Moina	4	±55.3	184.9
Cyclops	7	±48.5	136.0
Diaptomus	6	±54.6	172.8
Nauplii	8	±40.3	125.8

tion for the adults of the three species being about ±53%. For the four species of rotifers the average is ±46%, and that of the plants is about ±30%. As has been stated before the experimental error in case of the plants is probably large, and may account for a great part, or all, of the variation found. For the rotifers and the crustaceans the experimental error is much smaller, owing to the large portion of the sample counted and to the fact that the animals are more easily retained in filtering, the variation found consequently being due almost entirely to the uneven distribution. It is not probable that the small number of individuals that are sometimes found is sufficient to explain many of the variations, since in series H, where some of the species are very numerous, the variations are above the average.[7]

Direct observations were also made by examining the water surface for aggregates of animals. During the summer of 1915, before Moina appeared, crustaceans were frequently not seen for large areas but when they occured there were usually several together. On two occasions in August and September Moinas were present in the open water a few meters from the shore, so numerous that they could be seen from a distance of several meters. These "swarms" covered an area of about one-half to one meter in diameter while the surrounding water was almost free from these animals. Also when series H was collected two aggregates of crustaceans, chiefly Moina, were noticed in the center of Creel Bay. Here, however, the areas were larger than, and not as distinct as those near the shore. During the summer of 1916, such aggregates were seen on several occasions by Dr. Young and by the writer, both near the shore and out in the open water.[8]

Comparisons of the results With Those Obtained by Other Investigators

In every case that is known to the writer the collections for the study of the horizontal distribution of the plankton have been made with a plankton net and, with but few exceptions, have concerned only the total amount of plankton. These results usually show a small variation but tell nothing of the distribution of the individual species. As far as one can tell from the data for Devils Lake the distribution of the plankton as a whole in that lake seems to be similar to the distribution elsewhere.

A study of the subject was made on Lake St. Clair, Michigan, by Reighard in 1893.[9] He collected fourteen series, each consisting of two (in one case of three) successive hauls made in the same place. The volume of plankton per square meter of surface was then determined and the average amount in each series computed. In figuring the percentages of variation of the different catches from the average Reighard uses the volume of each catch as a basis while in this paper the average of the series is used as a basis. In order to make the results comparable the latter method has been applied to Reighard's data. For all but one series the plus and minus variations, and consequently also the mean variation, are the same since there are only two collections. Table XXII gives the plus or minus variation for each series as calculated from Reighard's data.

TABLE XXII

VARIATION PERCENTAGES OBTAINED FROM REIGHARD'S DATA

Series	II	Variation from mean in percent	±30.1
"	III	" " " " "	±17.0
"	IV	" " " " "	0.0
"	V	" " " " "	±13.9
"	VI	" " " " "	±14.6
"	VII	" " " " "	0.0
"	VIII	" " " " "	±5.4
"	IX	" " " " "	±3.1
"	X	" " " " "	0.0
"	XIII	" " " " "	±9.5
"	XIV	" " " " "	±4.3
"	XV	" " " " "	±14.7
"	XVI	" " " " "	±10.3
"	XVIII	" " " " "	±8.4
Average	value for all the series	" "	±9.4

In figuring the results by Reighard's method the variations of series II of the above series become +23.1% and −43.1%. The last variation is much greater than any other and Reighard states that it "is possibly sufficient to be referable to a 'swarm.' "

Similarly Apstein[10] studied the distribution in some of the German lakes by collecting thirty-one series, each of from two to five hauls. All the catches of a series were taken from equal depths from different parts of a lake. The catches (eighty in all) were undoubtedly all obtained from the pelagic zone at equal depths, but it is probable that the depth

of the lake differed at the different stations. The mean value of the variation from the mean of all the series is found to be ±5.5%, corresponding to ±9.4% for Reighard's data. The highest variation found by Apstein is +22.8%.

Apstein also counted the individual species in three series, (one of three and two of two catches) and reports some data published by Zacharias in 1895. From Apstein's data I computed the percentages for Diaptomus and Cyclops of two of the series, the catches of the third being made in widely different parts of the lake. Tables XXIII and XXIV give Apstein's figures together with the percentages.

TABLE XXIII

RESULTS OBTAINED FROM APSTEIN'S DATA FOR DOBERSDORFER SEE

(Amt.=number per cubic meter. % var.=variation from the mean in percent)

	Sample 27a		Sample 27e		Sample 27c		
	Amt.	% var.	Amt.	% var.	Amt.	% var.	Mean
Cyclops	122,088	+6.7	93,024	−18.6	128,016	+11.9	114,377
Diaptomus	328,320	−7.6	198,208	−44.5	539,947	+51.8	355,492

TABLE XXIV

RESULTS OBTAINED FROM APSTEIN'S DATA FOR GR. PLÖNER SEE

(% var.=percent of variation from mean)

	No. pr. catch	% var.	No. pr. catch	% var.	Mean
Cyclops	887	−1.5	915	+1.5	901
Diaptomus	26	−13.3	34	+13.3	30
Nauplii	372	+13.1	286	−13.1	329

In Dobersdorfer See Cyclops shows a mean variation of ±12.4% and a range of 30.5%. For Diaptomus the figures are: ±34.5% and 96.0%. In the case of Gr. Plöner See the variation for each catch and the mean variation are the same since there are only two series. The percentages are much lower than those for Dobersdorfer See.

In the series collected by Zacharias Hyalodaphnia has a mean variation of ±7% and a range of 15.7%, and the copepods a mean of ±5.9% and a range of 15.1%. (Table XXV). These figures, as well as those of Apstein, are much lower than the Devils Lake figures, and correspond more nearly with those obtained by Reighard and by Apstein for the total amount of plankton.

TABLE XXV

RESULTS OBTAINED FROM ZACHARIAS' DATA

Amt. = number per volume. % var. = variation from mean)

	Schlossgarten		Alesborg		Rott's Gart'n		
	Amt.	% var.	Amt.	% var.	Amt.	% var.	Mean
Hyalodaphnia	630	+10.5	540	−5.2	540	−5.2	570
Copepoda	720	−8.9	840	+6.£	810	+2.5	790
Bosmina	150	0.0	150	0.0	150	0.0	150

Kofoid[11] tested the longitudinal distribution of the plankton in Illinois River by making "a series of ten catches in immediate succession from a boat anchored in mid-channel." The current was flowing at the rate of nearly two miles an hour, and the time required for collecting was about two hours. The catches therefore represent plankton taken from a body of water about three miles in length. From the centrifuged material the volume of plankton per cubic meter was computed and the following percentages were obtained: mean ±3.6%, maximum +8.6%, minimum −5.5%, and the range 14.1%. Kofoid's results thus show a smaller variation than those of Reighard and of Apstein, but cannot very well be compared to samples obtained from a lake, especially during calm weather.

The distribution of Daphnia hyalina in Lake Geneva was studied by Gandolfi-Hornyold and Almeroth[12] during the summer of 1913. Vertical hauls were made with a net and the number of individuals in each catch were counted. All the catches taken from the same depth on the same day were then compared, regardless of the location and the depth of the lake at the place where the collections were made. From some data given by the authors the percentages were computed and are shown in Table XXVI.

TABLE XXVI

RESULTS OBTAINED FROM DATA GIVEN IN GANDOLFI-HORNYOLD AND ALMEROTH'S TABELLE I

Depth of Lake in m.	Depth of catch in m.	Number per catch	Mean	% var. from mean	Mean var. in %	Range of var. in %
40 E	10-0	E 3 E	24	E −87.5 E	±89.2	241.7
45 E		E 9 E		E −62.5 E		
15 E		E 41 E		E +70.8 E		
10.5 E		E 7 E		E −70.8 E		
17 E		E 61 E		E+154.2 E		
45 E	20-0	E 185 E	230.5	E −19.7 E	±19.7	39.4
E		E E		E E		
40 E		E 276 E		E +19.7 E		
40 E	30-0	E 236 E	284.5	E −17.0E	±17.0	34.0
E		E E		E E		
40 E		E 333 E		E +17.0 E		

The catches taken by hauling the net from a depth of ten meters show a large variation, but the percentages decrease as the depth and the number of organisms increase. In some cases the depth of the lake varies considerably but this does not seem to have any effect on the number of organisms.

"Swarms" or aggregates, similar to those seen in Devils Lake, have been discussed several times by different investigators, e.g. by Huitfeldt-Kaas,[13] Reighard,[14] and Ward.[15] The aggregates usually consist of Cladocera and in many cases they have been observed near the shore, but occasionally in free water. No great consideration is given them, however, since they are supposed to occur but seldom and therefore do not greatly effect the results of quantitative plankton studies. The comparatively irregular distribution shown by the zooplankton in Devils Lake is in all probability very constant since about the same results were obtained for all the series. The methods used are quite thoro and no large error is possible. It is significant, also, that both the Sedgwick-Rafter method and the pump method give about the same variation percentages in many cases. It is hardly conceivable that the organisms in Devils Lake should have a more irregular distribution than those elsewhere, but no work has been done that can be exactly compared to that

done on Devils Lake. Gandolfi-Hornyold and Almeroth's results show a large variation of Daphnia hyalina but the distances between the collecting stations were probably great and there were differences in depth and probably also in temperature. Apstein's and Zacharias' counts of the individual species show a distribution quite similar to that usually found for the total amount of plankton.[16] Catches made with a net, as in the above mentioned cases, represent the number of individuals in a vertical column of water, and it is possible that the vertical distribution for the different catches differed altho the total amount for the entire column differed but slightly from that of another column. If this were the case the horizontal distribution for the different levels would differ. The collections made in Devils Lake to test the vertical distribution (see table I) show a large difference in the number of animals of a column of water between two periods of collecting. Moreover when a large volume of water is collected, especially with a net, the differences in distribution tend to be reduced, since by this method several thickly populated portions of water may be included, while on the other hand the small sample usually collected for filtration in the Sedgwick-Rafter method may be obtained entirely either from a volume of water containing a "swarm" or from one where the organisms are scarce. This method is consequently the more precise for studying the local distribution of plankton forms.

Nor can the distribution of the total amount of plankton in Devils Lake be compared to that in other lakes, since the data for the former concern the individual species only. In the majority of cases it appears, however, that some species make up in volume or weight for the difficiency caused by others. Since the main portion of plankton usually consists of algae a large variation of the animals does not greatly effect the distribution of the plankton as a whole.

Conclusions

From the results obtained by the study of the horizontal distribution of the plankton in Devils Lake the following conclusions may be drawn:

(1) The zooplankton in Devils Lake shows a great irregularity in horizontal distribution, and this irregularity cannot be correlated with any variations in amount of phytoplankton or in the chemical and physical environment. It is more likely due to the habit of swarming among plankton animals, due perhaps to a social instinct, similar to that found

in many other groups of the animal kingdom. Plankton swarms are at times visible, even at considerable distances, to the naked eye.

(2) With larger samples (19 litres) the variations tend to be reduced, but even here they are at times greater than in the smaller ones (½ litre).

(3) Similar, tho in general smaller variations have been found by other workers, but no exact comparison with their results is possible, since their methods have been different.

(4) Definite conclusions regarding the distribution of the phytoplankton can not be drawn, owing to the inaccuracy in the method of its emuneration. In general, uowever, it appears to be more uniformly distributed than the zooplankton.

(5) These variations invalidate the usual assumption that a given sample of water is representative of a large area, at least in respect to its animal inhabitants, and necessitate the collection of large numbers of samples before definite conclusions regarding their distribution or movement can be drawn.

NOTES

[1] Owing to Mr. Moberg's absence on military duty in France, I have taken the liberty of editing his paper, adding some observations as footnotes and making a few changes in the text. The conclusions are mainly my own, but apart form these, and a few other minor alterations, the paper is his. R. T. Young.

[2] See Whipple "The Microscopy of Drinking Water." 1914, pp. 28 et seq.

[3] The chemical analyses were made by Dr. Fred H. Heath of the University of North Dakota.

[4] Whipple, *l.c.* p. 42.

Whipple, *l.c.* p. 41.

[6] In the Journal of the Quekett Microscopical Club, Vol. XI, pp. 373-4, Rousselet has described a new species of Brachionus from Devils Lake, under the name of spatiosus. As this form closely resembles B. mülleri, and numerous transitional forms occur, it is here included in the latter species. R. T. Y.

[7] In series H, only two litres of water were taken. In series I and J, in which 19 litres were taken, the variations are seen in general to be smaller than the average, as is to be expected. (Compare tables XVIII and XX and XXI) Even here, however, some of the variations exceed the average, while others are almost as great. (Compare the range of 184.6 for Diaptomus in series J, table XX, with the average for this genus of 172.8 in table XXI; Cyclops 121.2 in series I, table XVIII, with the average, 136.9 in table XXI, and Moina, 173.9 in series I with the average of 184.9 in table XXI.) In general, the more numerous the individuals of a species, the smaller the variations in their number. This also is to be expected. The variations in the phytoplankton

are probably partly attributable, as Mr. Moberg has stated, to experimental error. In part they are probably also due to chance variations in distribution. For example, in one case in which Nodularia was exceedingly abundant, I observed it clumped together in numerous small patches. If one or two of such masses happened to be included in a 500 cc sample, while another sample was free from them, they would readily explain the observed differences. Many of the variations in the zooplankton may also probably be due to chance, especially in those series where only 500 cc of water were filtered. Even so they indicate the difficulty, if not impossibility of obtaining reliable results by the Sedgwick-Rafter method, in the case at least of the zooplankton.

Such an assumption is, however, wholly inadequate to explain such a variation as is shown by Brachionus satanicus in samples 3 and 4, ser. D. table VII, in one of which 380 individuals were present in 500 cc, while another contained 0. Similarly 124 Pedalion were present in one of these samples and none in another. Vice versa, sample 3, in which no rotifers whatever occurred, contained 12 Cyclops, while sample 4, in which rotifers were abundant contained only 4 Cyclops. The comparatively few Cyclops present can hardly have determined the difference in number of the rotifers. The two samples were taken at points only about 200 metres apart in the main body of the lake which is roughly 15 x 7 Km in extent. The day was clear with but little wind and the physical and chemical conditions at the two stations were virtually identical, as may be seen in table VII. An explanation of such variations, as due either to chance or experimental error is, in my opinion, wholly excluded.

For further evidence of a similar character see Diaptomus, samples 2 and 4, ser. J, table XIX, in which 19 litres were sampled; Moina and Brachionus satanicus, samples 1 and 2 and Diaptomus, samples 3 and 4, ser. H, table XV, in which two litres were sampled; Brachionus Satanicus and Nauplii samples 3 and 4, Ser. E, table IX; Pedalion, samples 1 and 5 and Nauplii, samples 5 and 7, Ser. F, table XI, and Brachionus Satanicus, and Pedalion, samples 4 and 6, and Nauplii, samples 4, 6 and 8, Ser. G, table XIII.

These conclusions are furthermore supported by direct field observations. (See f.n. 8) R. T. Y.

[8] The following is from my notebook: "9–17–17. I notice copepod swarms very clearly today. In places, usually in streaks, the water is milky with Diaptomus, in others very few. Occurred at surface. Sunny . . . 9–18–17. I notice numerous copepod (mostly Moina) swarms in the surface water near shore, these forming streaks in the water visible plainly at a distance of several feet. I made a collection of one of these swarms, 500 cc, which I concentrated by filtering thru No. 20 bolting cloth. Collection made by simply dipping up some of the swarm in a quart jar. . . "

This collection when concentrated to 30 cc and counted gave approximately 70,000 individuals per litre! This number, moreover, is probably somewhat too low, owing to a number of the animals adhering to the pipette in transferring to the counting cell. R. T. Y.

[9] Reighard "A Biological Examination of Lake St. Clair," Bulletin of the Michigan Fish Commission, 1894, No. 4.

[10] Apstein "Das Süsswasserplankton, Methode and Resultate der quantitative Untersuchung," 1896, pp. 51 et seq.

[11] Kofoid "The Plankton of the Illinois River," Bulletin of the Illinois State Laboratory of Natural History, 1903, pp. 269 et seq.

[12] Gandolfi-Hornyold and Almeroth, "Mitteilungen über die Verteilung von Daphnia hyalina Leydig im Genfer See (Petit Lac), Internat. Revue d. ges. Hydrobiol. u. Hydrogr., 1915, Bd VII, pp. 426-432.

[13] Huitfeldt-Kaas, "Plankton in Norwegischen Binnenseen," Biol. Centralblatt, 1898, Bd XVIII, pp. 625 et seq.

[14] Reighard, *l.c.* p. 32 et Seg.

[15] Ward "A Biological Examination of Lake Michigan" Bulletin of the Michigan Fish Commission, 1896, No. 6, pp. 62-64.

[16] In the case of Cyclops and Diaptomus for Dobersdorfer See, Apstein finds a somewhat larger variation. The mean for Cyclops is 12.4%, and for Diaptomus 34.5%. For Diaptomus the maximum is +51.8% and the minimum —44.2%, making a range of 96%. In the 10-0 meter catches Gandolfi-Hornyold and Almeroth find a large variation, but in the catches from greater depths it is considerably smaller.